

THE BIOLOGY OF *EUPHASIOPTERYX BREVICORNIS*
(TOWNSEND) (DIPTERA, TACHINIDAE),
PARASITIC IN THE CONE-HEADED GRASSHOPPERS
(ORTHOPTERA, COPIPHORINAE)*

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The presence of oddly placed, supernumerary "spiracles" on a number of cone-headed grasshoppers [*Neoconocephalus r. robustus* (Scudder)] collected on Cape Cod in August, 1951, suggested parasitism by dipterous larvae, probably of some tachinid fly. Collection and confinement of a number of parasitized individuals during late summer in 1952 and '53 eventually led to the successful rearing of three male and two female flies. After considerable study, which involved not only these specimens but a large part of the accessible material in the difficult tribe Ormiini, C. W. Sabrosky of the Bureau of Entomology and Plant Quarantine is now describing the fly as a new subspecies of *Euphasiopteryx brevicornis*. (Sabrosky, in press). Reinhard in 1922 published a record of three larvae which emerged from an adult cricket, *Gryllus assimilis*, and formed puparia. Although no flies emerged, C. T. Greene identified the puparia as *Ormia* (now *Euphasiopteryx*) *ochracea* (Bigot). There is but one record of undoubted host relationship for the genus, that of "*E. australis* (Tns.)" as a parasite of the Brazilian mole cricket, *Scapteriscus vicinus* Scudder, reported by Wolcott (1940).¹ The cryptic habits of both host and parasite emphasized in the present paper further explain the scarcity and incompleteness of the previous life history data on these flies.

The locality where the parasitized cone-heads were

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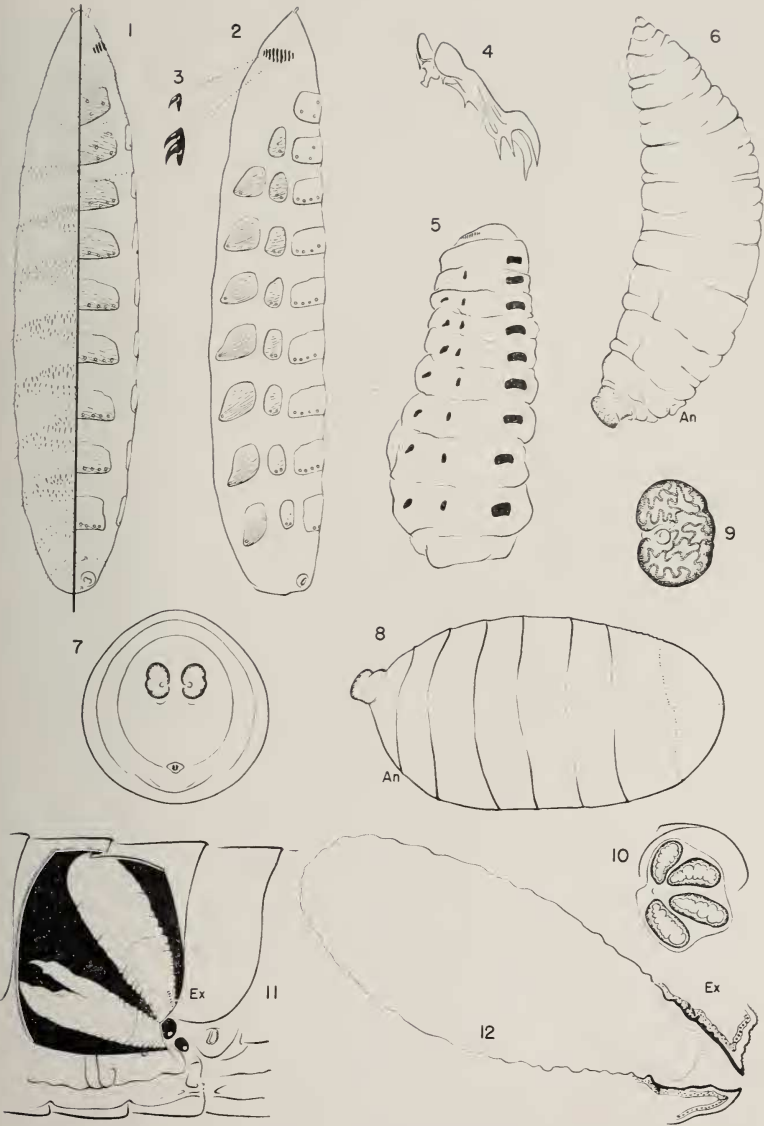
¹ *Australis* sensu Wolcott=*E. depleta* (Wiedemann), teste Sabrosky, 1953; *E. australis* (Tns.) from Peru is distinct. Hereafter, *E. australis* sensu Wolcott will be used in quotation marks.

collected is a narrow 16 acre tract, extending from the beachgrass-lined bay inland 0.4 mile to U.S. Route 6 in East Brewster, Mass. One fourth of the land bordering the beach is characterized by *Hudsonia*-lined sand-blows dotted with red pine, while the adjoining fourth is overgrown swamp. The remaining eight acres are largely open fields, supporting an occasional red cedar and bordered with clumps of bayberry and beach-plum. The cone-heads were confined to the beachgrass and open fields, although one or two specimens were taken in the bayberry bushes. Because of their alertness and habit of dropping from the tops of grasses and shrubs into inaccessible tangles below, the most practical collecting method is that of night-stalking. In early evening the ear-splitting, cicada-like song of a male is pin-pointed, then approached upwind; with careful maneuvering the singing insect may be spotted and grabbed or tricked into a ready net. Thus the taking of females is limited to chance sightings or association with singing males.

In this manner eight males were collected in the eight acre tract between 15 and 17 August, 1951; six were parasitized. On 3 August, 1952, seven males were parasitized of ten collected in the same area; three unparasitized males came from the beachgrass section. From the number of individual songs noted, probably at least 75 per cent of the male population in the tract were taken each season. The incidence of parasitism in this area, of the males at least, is certainly much higher than the one to five per cent

EXPLANATION OF PLATE 4

Euphasiopteryx brevicornis (Tns.). Fig. 1, left half, ventral aspect of 0.8 mm first instar larva; right half, dorsal aspect. Fig. 2, left lateral view of same, spines omitted. Fig. 3, detail of larval hooks. Fig. 4, first instar cephalopharyngeal skeleton. Fig. 5, 1.3 mm first instar larva after feeding. Fig. 6, nearly mature, 10 mm larva, An, anus. Fig. 7, posterior view of 8 mm puparium. Fig. 8, right lateral view of same. Fig. 9, detail of mature larval spiracular plate (x44). Fig. 10, detail of second instar spiracular plate (x457). Fig. 11, abdominal cutaway of the host, *Neoconocephalus r. robustus*, showing larval respiratory funnels in place; lower funnel was ruptured by escaping larva (x13). Fig. 12, longitudinal section of funnel showing larval posterior in place (dotted); Ex, first instar exuviae embedded in funnel wall (x40).



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reported by Wolcott (1951). A total of 50 larvae and vacated larval respiratory funnels was found in these 13 grasshoppers, an average of 3.85 per host. Two hosts contained one larva each, while two others contained eight and nine. Since all hosts were collected within three days in 1951 and on a single date in '52, the size range and probable age of the larvae are particularly noteworthy. In all specimens containing more than two larvae, considerable variation in larval size was found. This probably indicates different larval entry times, although it is also suggestive of feeding competition among the larvae. Two hosts which each contained one first instar larva, also contained six and seven other larvae of various sizes, including several three quarters grown. Another contained a first instar larva along with two more which were ready to pupate.

The dissection of three species of adult female ormiines by Townsend (1911) indicates that larviposition may be the rule with these flies. It is not known whether the females deposit their larvae directly on the host insects, or merely on ground or vegetation frequented by them. The armored, planidium type first instar larva (figs. 1 and 2), coupled with the following observations, suggests an active seeking out of host by larva. Four of the cone-heads collected contained first instar larvae, one of which was found in the muscles of the right hind femur, one quarter of the femur length from the coxa. This cone-head had been killed and pinned, so that even though the larva was found headed apically in the femur, there is no assurance that this was the case before death. Although it is tempting to speculate that it had entered the host through soft or membranous areas of the tarsus, it might be argued that it had entered at any other point and become diverted into the leg in making its way to the abdomen.

On the other hand, a careful autopsy of seven cone-heads showed that not one of 30 larvae was encountered in any part of the body but the abdominal cavity. Twenty more larvae, or larval funnels, in the six other cone-heads were also restricted to the abdomen. The second first instar larva was found near the anterior end of the mid gut, and the third in a tangle of malpighian tubules, both free in the

haemocoel. The fourth larva (fig. 5) had recently become fixed to the pleural membrane on the left side of the fifth abdominal segment. This evidence suggests that the larvae are strongly attracted to the host's abdominal haemocoel, and that they probably do not often miss this goal. It is possible that entry may occasionally be effected via vulnerable areas of the appendages in contact with the ground. In any case, the paired sets of hooks on the second segment (fig. 3) undoubtedly assist the larvae during penetration of the host.

There was no apparent evidence of larval entrance on any of the 13 parasitized cone-heads, although it might be mentioned that five bore from one to four 0.5 to 1.5 mm scars on either or both faces of their hind femora. No such scars were found on the uninfected specimens. They may be significant, but it would be difficult to understand how or why the larvae would enter at such a point. It is more likely that these scars were earned during battle with other males, or perhaps during or after mating.

Although not exactly popular knowledge, the unusual respiratory funnels used by tachinid larvae for obtaining an atmospheric oxygen supply have long been known from the early biological researches of Nielsen (1909) and Pantel (1910). Baer (1920), Thompson (1928), and Beard (1942), have also contributed to our understanding of larval respiration and host relationships within this group of flies. (See Clausen (1940) for a comprehensive review.) York and Prescott (1952) have reported that similar funnels are also formed by nemestrinid larvae in grasshopper hosts. *Euphasiopteryx* behaves typically for, after the active larva enters the cone-head's abdomen, it perforates the host's body wall and settles down with its posterior spiracles in contact with the outside air until it is nearly ready to pupate. Perforation of the host integument may be accomplished by means of the minute circumstigmatal spines as suggested by Beard, or in the case of larvae such as these, perhaps by means of the postcephalic recurved hooks. In any event, the larva, with its spiracles in this hole, obstructs the normal healing of the wound in such a manner as to cause an inward growth of host integument which eventually

forms a funnel around its posterior end (see Beard, 1942).

With *Euphasiopteryx*, the funnel walls are extended by a brownish, transparent, acellular membrane, so that the larva is completely enclosed in a sac-like structure (figs. 11 and 12). This type of funnel has been described for certain other tachinids, and Nielsen (1909) claims that the saccular portion is composed of the compacted walls of host fat body cells destroyed by the larva. Pantel (1910) presumed that the enclosed larva fed on the host's body fluids absorbed through the sac walls. However this may be, he stated that at a later stage such larvae pierce the sheath and feed actively on fat body and other tissues. This may be the case with *Euphasiopteryx*, for most over 6 or 8 mm long had ruptured their sheaths (fig. 11).

In the cone-heads examined, all the darkened external funnel openings were situated either in the soft pleural integument or in the ventral intersegmental membranes, from the first through the eighth abdominal segments (fig. 11). Internally the basal 1 or 2 mm of the funnel bear heavily sclerotized annular thickenings (fig. 12), while the whole structure is often enveloped in the lobular fat body, covered with blood cells and detritus, and wound round with malpighian tubules. The first instar exuviae (figs. 11 and 12, Ex) are embedded in the thickened layers of cuticle at the funnel base, but no trace of later molts has been found. Cast larval skins of the squash bug parasite, *Trichopoda pennipes* Fabr., have been found either embedded in the sheath or, more commonly, between the maggot and its sheath (Beard, 1942).

Although the remarkable first instar larvae of *Phasipteryx montana* Tns. [*E. ochracea* (Bigot)] and *P. bilimeki* BB. [*E. bilimekii* (BB.)] were described and figured by Townsend (1912, 1942), drawings of this stage of *brevicornis* are included here for comparison. This active, armored larva (figs. 1 and 2), shortly after entering the host, measures about 0.8 x 0.15 mm. It has already done sufficient feeding so that the nine dorsal plates and the flanking rows of eight dorsolateral and seven ventrolateral plates no longer overlap as shown by Townsend. The light brown plates are sculptured, and bear a pattern of round,

unpigmented spots. These hole-like dots form triangular patterns on the first two dorsal plates as described for *E. ochracea* by Townsend. In the present well preserved material, the spots do not appear to be origins of detached bristles as he suggested. Ventrally the abdomen is equipped with six compact groups of long spines instead of plates, while posteriorly and anteriorly the body is ringed with bands of microspines. The last segment, adorned with a few larger spines, bears the slightly raised spiracular plates which are bounded anterolaterally by a lightly pigmented area. Anteriorly there is a group of claw-like spurs on either side of the second segment, similar to those described for *E. bilimekii*. Each group is made up of nine heavily sclerotized rods, the seven median ones each bearing two hooks, and the end rods, one each (fig. 3). The cephalopharyngeal skeleton (fig. 4) extends back to the anterior margin of the first dorsal plate. The antennae are rather prominent elongate papillae. After considerable feeding, and at the time it becomes sedentary, this larva measures about 1.3 x 0.8 mm, and appears as shown in fig. 5.

Mature larvae, ready to pupate (fig. 6), are typical white maggots and measure from 9 x 3 to 13 x 4.5 mm. They are practically smooth, although segmental bands of minute spines become barely visible at 90x in sectioned material. The pair of large, well separated posterior tubercles which bear the spiracles are shining black. The reniform spiracular plate (fig. 9) bears an inconstant serpentine pattern of minute parallel ridges. Between these ridges is a single row of breathing pores leading to the atrium within the tubercle. The stigmatic scar, representing the spiracle of the previous instar, is eccentrically placed opposite the hilum on the plate's inner margin. Figure 10 is a detail of the typically muscoid spiracular plate of the second instar larva. Prominent fleshy lobes mark the anal opening (An) which is rather remote from the spiracles.

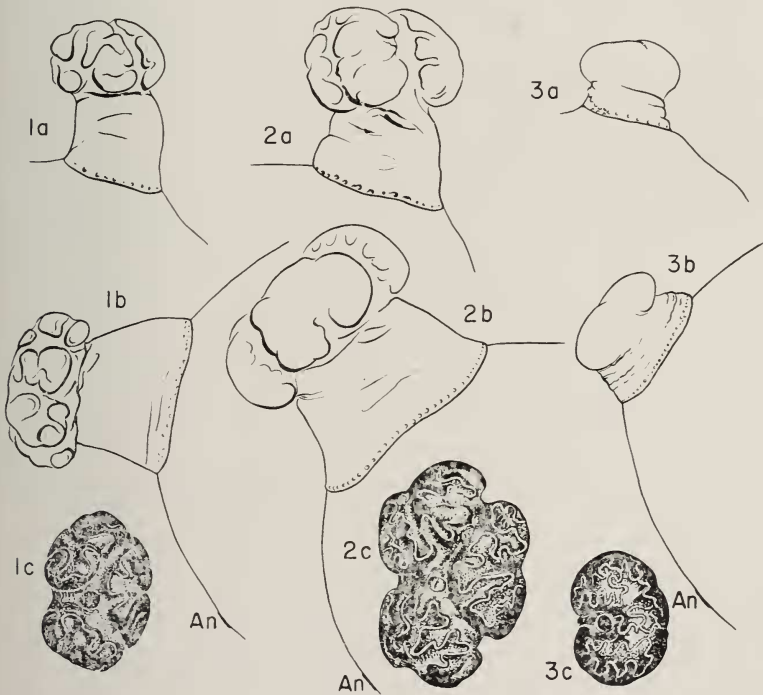
From the 13 cone-heads collected and confined, 12 larvae escaped and successfully formed puparia. When ready to pupate the larvae pierced the host's integument, generally in the vicinity of their breathing funnels, although one may have emerged from the anus. They were given a choice of

moist or dry, loosely packed earth with piles of dead grass for cover. The larvae were exceedingly active, humping frantically over the soil and exploring every part of the chamber. Some burrowed between or under loose, moist clods, but most of them settled under the grass on the moist surface. Within one to six hours all had become shortened and dark brown; puparia were formed a few hours later. One large specimen emerged from its host and formed a puparium within one hour.

As to the effects of the parasitism on the host, most of the cone-heads were active, singing and feeding nightly, until a day or two before the larvae emerged. A few hours before the exodus they became feeble and sluggish; two or three hours after even one or two larvae had emerged, the host was dead. Post-mortem examination showed a depletion of the fat body roughly proportionate to the number of parasites, but little apparent damage to the major organ systems. From these facts it is significant that larval survival is narrowly limited to those individuals within a particular host which reach maturity almost simultaneously. Two larvae emerged from one host within two hours of each other and pupated, while six other larvae, including one of the first instar, died inside the moribund host a few hours later. The total complement of three larvae escaped from another host and pupated successfully. This situation, involving larvae in staggered developmental stages within one host, is suggestive of a rather extended period of larviposition and a considerable endurance in the host-seeking first instar larvae. It might be added here that two heavily parasitized hosts also contained one and two specimens of a nematomorph, *Gordius* sp., coiled in their abdominal cavities. Further, three of the 1952 cone-heads each contained one nearly mature larva which Mr. Sabrosky has suggested as possibly *Beskia aelops*.

A female puparium is shown in figs. 7 and 8. Four male puparia vary from approximately 5.5 x 2.9 to 6.2 x 3.4 mm, and those of two females from 5.3 x 3.1 to 8.1 x 4.1 mm. The surface is finely wrinkled and the larval segmentation is fairly prominent. The line of dehiscence of the puparial cap, as well as a secondary fracture, is dotted in the figure.

Although Green figured the puparium of *Oestrophasia* (= *Euphasiopteryx*) *ochracea* in 1922, spiracular details of the three known puparia of the genus are included in text fig. 1 for ready comparison. The *brevicornis* puparium is dark mahogany with the spiracular tubercles a shining black, while those of *ochracea* and *depleta* are a dull brick red with subshining black tubercles. In all three species the tubercles are basally enlarged and well separated, *depleta* being the most extreme in these features. The tubercles of *ochracea* arise slightly above the longitudinal puparial axis, but in *depleta* they arise obliquely from the



Text figure 1. Comparison of spiracular details of the three known puparia of *Euphasiopteryx*. Fig. 1, *E. ochracea* (Bigot); a, ventral aspect of right spiracular tubercle; b, lateral aspect of same, An, anus; c, detail of spiracular plate. Fig. 2, *E. depleta* (Wied.), a, b, c, same as fig. 1. Fig. 3, *E. brevicornis* (Tns.), a, b, c, same as fig. 1. (x44).

posterior dorsal surface. In *brevicornis* the tubercles arise from an intermediate position well above the axis. The serpentine pattern of respiratory pores on each spiracular plate is raised in *ochracea* and *depleta*, and is divided into three groups which are only vaguely indicated in some specimens of *brevicornis*. These groups in *depleta* are separated by much deeper grooves than in *ochracea*. The stigmatic scar is fairly prominent and the anus is remote from the tubercles in all three species.

All puparia of *brevicornis* were formed in the laboratory essentially under normal seasonal temperatures. Two were obtained on 21 Aug., 1951, and ten more between 5 and 12 Aug., 1952. Each year the puparia were kept at about 23° C for a little over two months, held at 8° for two more months, then returned to 23°. Of the 1951 puparia, one female emerged on 10 March, 1952; the other, also a female, succumbed to mold shortly before emergence. Of the 1952 puparia, two males emerged after 11 days, and one male and one female emerged after 12 days, all before being placed in the cold room. The remaining six succumbed to mold and anthomyiid larvae in the insectary after cold treatment. Three of these contained fully formed flies, at least one of which was a female. Townsend (1936) cited a case of *E. ochracea* (Bigot) adults emerging in October, 12 days after the puparia were collected in Dallas, Texas. According to Wolcott (1951) the pupal stage of "*E. australis* (Tns.)" in Brazil lasts for ten days.

From these records it is evident that a diapause induced by winter cold is not necessary for adult development. On Cape Cod, adults of both *Neoconocephalus robustus* and *ensiger* have been taken at least until early October, while adults of several other likely orthopteran hosts, such as the katydid, *Amblycorypha oblongifolia carinata* R. & H., and the common cricket, *Acheta assimilis* F., live beyond mid-November in many seasons. In the vicinity of Dallas, the closely related *N. triops* (L.) has been collected in mid-December (Rehn and Hebard, 1944), and there are certainly many other possible hosts available beyond this date. With the probable capacity for a four to five week life cycle as far north as Cape Cod, this parasite could well produce

at least two generations a year on adult Orthoptera alone. It can and probably does pass the winter in the puparium, although nothing is known of the mating habits and survival capabilities of the adult flies.

In an effort to fill in the range and determine the host preferenda of these little-known flies, 15 specimens of *N. r. robustus* in the Museum of Comparative Zoology, from Cape Cod to Long Island, were examined for the presence of larval breathing holes. Similarly examined were 176 specimens, representing nine other species of *Neoconocephalus* from Massachusetts to Minnesota, Texas, and Florida, together with 26 Florida specimens of the related genera *Belocephalus*, *Pyrgocorypha*, and *Homorocoryphus*. In addition, large numbers of Orthoptera have been collected in East Brewster for anatomical studies over the past five years, and lately re-examined. These have included such likely hosts as *N. ensiger* (Harris); the conocephaline, *Orchelimum vulgare* Harris; the phaneropterine, *Amblycorypha oblongifolia carinata* R. & H.; and the common cricket, *Acheta assimilis* F. All of these examinations proved negative except for a single male of *N. ensiger*, collected by Richard Dow in Needham, Mass., 7 Aug., 1936, which bore the characteristic larval breathing hole in the left pleural membrane of the sixth abdominal segment. After softening the specimen a half-grown larva, with the first instar exuviae adhering to the funnel, was dissected out. On comparison with equivalent material under study, there is little doubt that *E. brevicornis* also parasitizes *N. ensiger*.

C. W. Sabrosky has checked the ranges of the two subspecies of *E. brevicornis* against those of the two subspecies of this particular host, *N. r. robustus* and *r. crepitans*, and informs me that the ranges show no significant coincidence. Therefore, until further evidence is available, it is assumed that the two subspecies of *brevicornis* must utilize additional hosts, at least in other areas of the range, but one or more of the ten other species of *Neoconocephalus* are probably favored. The question as to whether or not only adult Orthoptera are parasitized remains unanswered. Should the adults of a certain species

be the only host in a particular area, either the pupal stage or the adult life must be rather extended; on the other hand, if nymphal stages are also attacked, the host attrition must be considerable in favorable seasons.

Since all evidence has shown the genus to have a predilection for nocturnal orthopteran hosts, it is not surprising that, in the laboratory at least, the adult flies are also nocturnal. Wolcott (1951) has reported that "*E. australis*" adults hid in the darkest part of their cage during the day, but were unusually active at night. At present I can only confirm his observations and add that, during six years of occasional general collecting in the East Brewster area, I have never seen an adult fly. Many specimens seen by Mr. Sabrosky were collected at night, a further hint, but not proof, of nocturnal habits. Although much of the evidence cited above on range and host preference is either negative or purely circumstantial and speculative, it does explain the rarity and obscurity of these flies as well as their extremely local occurrence.

I extend my appreciation to C. W. Sabrosky of the Bureau of Entomology and Plant Quarantine for furnishing some of the pertinent references included, and especially for identification of the fly and description of the new subspecies, without which this information would be of little value. He made available for comparison the puparia of *E. ochracea* and *australis*, details of which are shown in text fig. 1. I also wish to thank Prof. H. J. Reinhard, of the Agricultural and Mechanical College of Texas, for his part in assisting in the identification.

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